..m) are constants. Then as in the above case we show that the linear element can be put in the form

$$ds^2 = (dx^1)^2 + \ldots + (dx^m)^2 + g_{ij} \, dx^i \, dx^j \quad (i, j = m+1, \ldots n),$$

where g_{ij} are independent of $x^1, \ldots, x^m$. When $m = n - 1$, equation (6.7) is reducible to the euclidean form.

7. If A^i are the contravariant components of a vector in a Riemannian geometry, its covariant components A_i, are given by

$$A^i = g^{i\alpha} A_\alpha. \tag{7.1}$$

When this expression is substituted in (3.1), we obtain

$$\frac{\partial A_i}{\partial x^j} - \Gamma_{ij}^\alpha A_\alpha - A_i \frac{\partial \log \varphi}{\partial x^j} = 0. \tag{7.2}$$

When we are dealing with a non-Riemannian geometry we say that a field of parallel covariant vectors is one which satisfies (7.2).

The conditions of integrability of (7.2) are

$$A_\alpha B_{ijk}^\alpha = 0. \tag{7.3}$$

In order that the A's given by (7.3) shall satisfy (7.2) it is necessary that

$$A_\alpha B_{ijkl}^\alpha = 0. \tag{7.4}$$

As in the case of contravariant vectors, it can be shown that when there are m ($< n$) independent sets of solutions of (7.3) which satisfy (7.4) there exist m fields of parallel, covariant vectors.

The methods of §§ 4, 5 cannot be applied to the case of covariant fields.

ON THE INFLUENCE OF DENSITY OF POPULATION UPON THE RATE OF REPRODUCTION IN DROSOPHILA[1]

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It has long been known that degree of crowding of organisms in a given space, or the density of the population, has an influence upon various vital processes of the individuals composing the population. In the matter of growth Semper[2] and before him Jabez Hogg[3] showed that volume of water apart from food and other conditions has an influence upon the rate. This subject has again been studied recently by Bilski[4]. Farr[5] showed that there is in man a definite relation between density of population and the death rate. This old work of Farr's has recently been gone over carefully and confirmed by Brownlee.[6] Drzwina and Bohn[7] show that a particular concentration of a toxic substance, just lethal for a single

individual in a given volume of water (working with such organisms as infusoria, planarians, hydra, tadpoles, etc.), will be sub-lethal if several individuals are present in the same fixed volume of water.

Without undertaking at this time any systematic review of the literature on this subject it is our purpose in this paper to present some experimental data on the influence of density of population upon a different biological function than those mentioned above, namely specific reproductive rate. This variable we define as measured by the number of adults (imagoes) produced per mated female per day over a specified period. Our interest in this problem arose originally from purely practical considerations. Anyone doing experimental work with *Drosophila* has constantly arising this situation: he wishes to start an experiment with a large number of flies of homogeneous make-up as a group. What is the most expeditious way to get the desired numbers while still maintaining the requirement of homogeneity? Is it better to mate a considerable number of pairs in one bottle, to furnish the desired progeny, and if so, how many pairs? Or is it better to mate up one or two pairs only in each of several bottles? Which plan will give the largest progeny group? Not being able to answer this practically important question satisfactorily either by *a priori* reasoning, or by perusal of the *Drosophila* literature, it was decided to test it experimentally. The results proved to have a considerably wider interest than that implied in the purely practical question.

Plan of Experiment.—Mass matings were made on March 21, 1921 of flies from our line 107, the characteristics of which have been described by Pearl and Parker.[8] When the offspring from the matings emerged they were used to make up the matings of this experiment, according to the following plan. Half pint milk bottles were used, and the food arrangements, etc., were according to the standard *Drosophila* technique of this laboratory, fully described by Pearl and Parker.[9] The composition of the matings was as follows:

SERIES	NO. OF BOTTLES	MATED PAIRS IN EACH BOTTLE AT START	SERIES	NO. OF BOTTLES	MATED PAIRS IN EACH BOTTLE AT START
1	4	1	9	4	9
2	4	2	10	3	10
3	4	3	11	3	12
4	4	4	12	3	15
5	4	5	13	3	20
6	4	6	14	1	25
7	4	7	15	3	30
8	4	8	16	2	50

These bottles were put into a 25° incubator. At the end of 8 days the parent flies still surviving were transferred to fresh half pint bottles and allowed to continue breeding for a second period of 8 days.

All the progeny flies as they emerged, as imagoes from the two series of bottles were counted and recorded as to sex. No account was kept of larvae or pupae. We are dealing here with net reproductive capacity, just as in certain of our poultry work (Pearl[10]). Food and temperature conditions were constant for all bottles throughout the experiment. The only significant variable between the several series was the density of population. There occurred various accidents to some of the bottles in the course of the experiment. Some of the mated flies died; food occasionally rose in the bottles and killed a few individuals, etc. In reducing the results to a per ♀ day basis allowance has been made for these accidents, and the final results set forth below represent the outcome for normal mated flies living under normal conditions.

Inasmuch as only 16 day's progeny was counted the results cannot be directly stated in terms of total reproductive capacity. Instead they have been tabulated as the rate of reproduction per ♀ day over a 16 day period after emergency. It is quite certain however that the absolute number of progeny per ♀ in the first 16 days of life is highly correlated with the unknown total reproductive capacity. This we feel sure of from many observations in *Drosophila* and from analogous observations on fecundity in the domestic fowl.

Results.—The results of the experiments are exhibited in Table 1, and graphically in figure 1. The table contains the following data: (*a*) the numbers of mated pairs per bottle at the start. The numbers of mated flies per bottle were therefore twice these figures at the start; (*b*) the mean population of mated flies over the whole period of 16 days. If no accidents had occurred these figures would have been 2, 4, 6, 8, 10, 12, 14, 16, etc. But accidents and deaths did occur. The figures set down represent the actual average number of flies present in each bottle over the period of the experiments, taken as a whole. (*c*) The mean number of flies per cubic centimeter of free air space in the bottle. Since all the bottles were by careful measurement of the food made to contain the same number of cc. (130) of free air space, it follows that the entries in this column are simply a constant ($1/_{130}$) times the entries in the preceding column. They are inserted merely to show what the actual density in these experiments was. (*d*) The mean number of flies per square centimeter of agar, growing yeast on its surface, in each bottle. The same remarks apply to this as to the cubic density figure. It corresponds exactly to the density of population figure used in human vital statistics. The food area per bottle was 23.76 cm.² (*e*) The total female days, meaning the number got by adding together for all females the number of days that each was in the experiment. Thus if a female lived throughout the experiment she contributed 16 ♀ days (1×16) to the total; if she lived 7 days she contributed 7 ♀ days (1×7) and so on. (*f*) Total absolute number of

imagoes produced in 16 days. These absolute figures vary of course with the accidental circumstances affecting the mated population. (*g*) The observed rate of reproduction, given as number of offspring imagoes per mated female per day. (*h*) The theoretical rate of reproduction (number of imagoes per mated female per day) as calculated from equation (*i*) below.

TABLE 1

EXPERIMENTAL DATA

PAIRS PER BOTTLE AT START	MEAN POP. AVERAGE 16 DAYS	MEAN FLIES PER CM³ OF SPACE	MEAN FLIES PER CM² OF FOOD AREA	TOTAL ♀ DAYS	TOTAL IMAGOES IN 16 DAY	IMAGOES PER MATED♀ PER DAY	*y* FROM EQUATION (i)
1	2.00	.015	.084	63	1348	21.4	21.1
2	3.40	.026	.143	89	1124	12.6	14.5
3	5.50	.042	.231	173.5	1877	10.8	10.2
4	7.32	.056	.308	232	2100	9.1	8.1
5	9.29	.071	.391	267	1585	5.9	6.7
6	10.29	.079	.433	298.5	2034	6.8	6.2
7	11.51	.089	.484	377.5	1951	5.2	5.6
8	14.48	.111	.609	436.5	1996	4.6	4.6
9	16.62	.128	.700	519	2117	4.1	4.0
10	18.74	.144	.789	275	855	3.1	3.6
12	21.70	.167	.913	504	1746	3.5	3.1
15	26.02	.200	1.095	609.5	1389	2.3	2.5
20	34.02	.262	1.432	754	1666	2.2	1.8
25	47.75	.367	2.010	384	388	1.0	1.1
30	47.73	.367	2.009	1069.5	1272	1.2	1.1
50	90.66	.697	3.816	1446.5	474	.33	.34

It is at once apparent from this table that there is a profound and regular change in the rate of reproduction of *Drosophila*, under the conditions of these experiments, with increasing density of population. The rate of reproduction per mated female per day declines as density of population increases, at first extremely rapidly and then more and more slowly at higher densities. The total number of progeny flies (23,922) is great enough to give confidence in the results.

A better appreciation may be obtained of the nature and regularity of this change if we put the results in graphic form. This is done in Fig. 1.

The smooth curve passing through the circles is the graph of equation (i) fitted to the observations by the method of least squares. In this equation *y* denotes imagoes per mated female per day, and *x* denotes mean density of the mated population (measured as flies per bottle) over the whole 16 day period.

$$y = 34.53 \, e^{-.018x} \, x^{-.658} \tag{i}$$

Or, in logarithmic form,

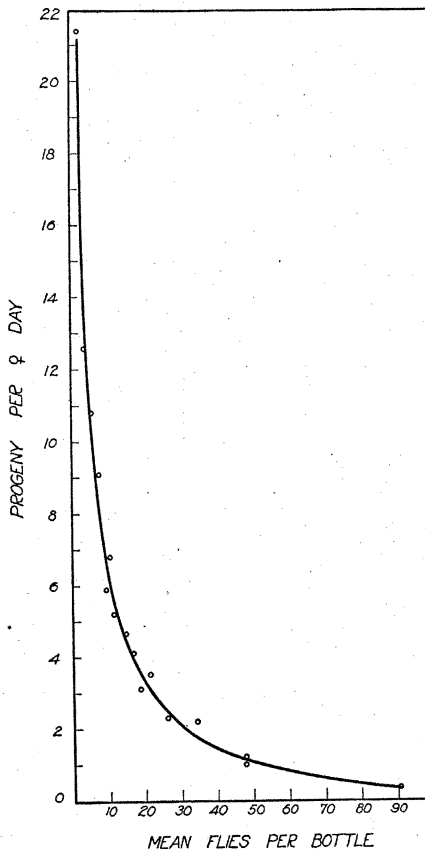$$\log y = 1.54 - .008 \, x - .658 \log x \tag{ii}$$

FIG. 1

Showing changes in rate of reproduction of *Drosophila* with increasing density of the mated population. The circles give the observations and the smooth curve is thegraph of the logarithmic equation discussed in the text.

It is at once apparent that this equation describes the observed facts with extraordinary precision. Rarely, even in a physical or chemical experiment, does one get such close agreement as is here shown between observation and theory. Plainly the curve is the expression of the law relating these two phenomena, rate of reproduction and density of population.

It is of interest to note that this equation is essentially identical in form with Farr's Law relating death-rate to population. Farr's original equation was the following, put in logarithmic form:

$$\log D = \log a + k \log d$$

where D denotes death-rate and d density of population and a and k are constants. Brownlee has slightly modified the constants but the essential form remains the same. Now in our equation (ii) the term in x is obviously of no practical importance, and could be left out entirely without visibly affecting the fit. It was only put in in a spirit of meticulous curve-fitting accuracy. With this term out our equation becomes in form identical with Farr's except that we have shifted the origin. The only essential difference is that in his case death-rate is shown to vary directly with density of population, while in the present case rate of reproduction varies inversely with density, but according to the same law. Death and reproduction are both fundamental and antithetical biological phenomena. What we know about the matter suggests that density of population has a profound effect upon many if not all general and fundamental biological processes. Brownlee points out that the same law holds in racing for the relationship between the record time for any definite length of course and the length itself, and for other biological and biochemical phenomena.

Bilski (*loc. cit.*) uses essentially the same equation to describe the influence of density of population and growth in tadpoles. Certainly the subject deserves further study. Possibly our present results offer a clue to a part at least of the solution of the problem of the practically world-wide decline in the birth-rate which had been going on for more than a quarter of a century before the outbreak of the war.

Discussion.—How can the result be explained? The extreme closeness of the observations to the theoretical curve indicates clearly that we are dealing here with no haphazard performance, but with a highly lawful phenomenon. The first point that occurs to one is that since we are dealing with imagoes only, the result may perhaps be explained by larval and pupal elimination due to overcrowding in these stages. In the bottle say with 20 females there were laid, on this view, something like 20 times as many eggs as in the bottle containing one female, these eggs developed into 20 times as many larvae, there was not room or food for so many larvae, therefore many of them were selectively eliminated, and the survivors which got through to the imago stage indicated only a low reproduction rate, which represented however only the capacity of 80 cc. of banana-agar or 23.76 cm.^{2} of food surface to nourish larvae, and nothing else.

Plausible as this hypothesis is—the more so because it would at once indicate why our rate of reproduction variable follows Farr's Law, since it would mean Farr's Law applying to the larvae—it cannot possibly account for the facts. To demonstrate this we have only to examine with some care the absolute figures given in the fifth column of Table 1. In the first place let it be recalled that the greatest drop in rate of reproduction (imagoes per ♀ per day) occurs as we pass from a mean density of 2 flies per bottle to one of 3.4 flies per bottle (1 and 2 pairs originally). The next greatest drop in the rate is from the bottles of density 3.40 to those of density 5.50. Now at all these low densities one in fact cannot possibly speak of larval crowding at all. This anyone knows who has experimentally bred *Drosophila*. A half-pint bottle with 80 cc. of banana-agar will support many more than all the larvae one or two or three females will produce in 8 days. This is indicated by the absolute figures in the fifth column of Table 1. The bottles containing 9 mated pairs at the start produced 2117 offspring imagoes. Therefore the food was sufficient to allow at least that many larvae to come through successfully. But in the bottles with 1, 2, or 3 mated females the absolute number of larvae was much less than this. Now the drop from the one pair to the two pair bottles in rate of reproduction was 8.8. To prove that this cannot be explained by larval crowding and elimination we have only to multiply 21.4 the rate per ♀ day in the 1 pair bottles, by 89 the number of ♀ days in the 2-pair bottles. This will give the number of imagoes which would have been produced in the 2-pair bottles had the reproduction rate of the

1-pair bottles held there. The result is 1904.6. *But this is 200 or more less than the absolute number produced in various other bottles.* Therefore the drop in the rate from the 1-pair to the 2-pair bottles cannot be explained on the supposition of larval crowding and elimination. Possibly this factor comes into play in the higher densities, though there is no evidence as yet that such is the fact.

That density of population influences fecundity in the same sense that it is here shown to affect rate of reproduction was demonstrated with fowls more than a decade ago.[11] It was found that there was a steady decline in mean annual fecundity in Barred Rock pullets as one increased the number of birds per year from 50 to 100 and to 150. The experiments were so arranged that the square feet of floor space per bird (that is to say the density of population in Farr's sense) was substantially identical in all three sets—exactly so in the case of the 50 and 100 bird pens, and only slightly less so in the 150 bird pens. We cannot go into the details of these careful and critical experiments with poultry here, but would point out that they indicate that there is apparently another element involved in the case besides mere physical density, which element in our ignorance we may perhaps tentatively call psychological. Apparently there is a physiological effect of keeping large numbers of individuals together in a confined area or space, even though the amount of space or area *per individual* is identically the same in the large crowds of individuals as in the small crowds.

In general there can be no question that this whole matter of influence of density of population, in all senses, upon biological phenomena, deserves a great deal more investigation than it has had. The indications all are that it is the most important and significant element in the biological, as distinguished from the physical, environment of organisms.

Summary.—In this paper it is shown that the rate of reproduction of *Drosophila* during the first 16 days of its imaginal life varies inversely with density of population, in an extremely exact manner, in accordance with the following equation which is essentially an inverse form of Farr's Law,

$$\log y = a - bx - c \log x.$$

[1] Papers from the Department of Biometry and Vital Statistics, School of Hygiene and Public Health, Johns Hopkins University. No. 57.

[2] Semper, K. *The Natural Conditions of Existence as they Affect Animal Life.* Fourth Edit. London 1890. (Other references to detailed papers are given in this book.)

[3] Cited from Semper, *loc. cit.*

[4] Bilski, F. *Pflüger's Arch.* **188**, pp. 254–272, 1921.

[5] Farr, Wm. *Decennial Suppl. Reg. Gen.* 1861–70.

[6] Brownlee, J. *J. Roy. Stat. Soc.* **82**, pp. 34–77, 1919, and **83**, pp. 280–283, 1920.

[7] Drzwina, A., and Bohn, G., *C. R. Soc. Biol. Paris*, **84**, pp. 917–919, 1921.

[8] Pearl, R. and Parker, S. L. *Amer. Nat.* **56**, pp. 174–187, 1922.

[9] Pearl, R. and Parker, S. L.   *Amer. Nat.* **55,** pp. 481–509, 1921.

[10] Pearl, R.   *Genetics.* **2,** pp. 417–432, 1917.

[11] Pearl, R. and Surface, F. M.   *U. S. Dept. Agr. Bur. Amer. Ind. Bulletin* No. 110, Part 1, pp. 1–80, 1909.

ANIMAL EVOLUTION

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There are few lines of scientific speculation of such general interest as the problem of the evolution of the varied assemblage of types included in the animal kingom, while at the same time a logical and detached consideration of this problem is rendered exceedingly difficult both because of the isolated position occupied by many of these types and by the conviction we all have that man must represent the highest of them.

But while undoubtedly man is the most efficient and the dominant member of the animal kingdom it by no means necessarily follows that he and his fellow vertebrates are from the strictly biological standpoint the most perfect.

In the following pages I shall indicate, as briefly as possible, a line of reasoning whereby all the various animal types are brought into correlation with each other, and their evolution is shown to be not evolution in the sense of a progressive development from a lower type to a higher, but instead the gradual acquisition of increasing economic efficiency through the progressively greater and greater departure from biological perfection, correlated with the gradual loosening of the bonds by which the most perfect type is economically handicapped.

In a very large and important group of animals, the Protozoa, the body is composed of a single cell; but in all animals except the Protozoa the body is composed of a very large number of cells which are differentiated to serve definite purposes.

All multicellular animals begin life as a single cell. As at this stage they are in this respect comparable in structure to a protozoan, in later life they may be assumed to represent an advance over the protozoan type.

The original cell giving rise to a multicellular animal typically divides into two, four, and eight similar cells, the cleavage taking place in three planes each at right angles to the other two; each of these eight similar cells continues to divide until a hollow ball is formed of numerous cells all of which are alike. Such a structure is represented by a blastula, but no adult animal (? except *Salinella*) which can be regarded as the equivalent of such a stage is known.